Notes on the Life Cycle and Natural History of Butterflies of El Salvador. I B.—*Hamadryas februa* (Nymphalidae-Hamadryadinae)

Alberto Muyshondt and Alberto Muyshondt, Jr.
101 Ave. N. 322, San Salvador, El Salvador

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Abstract: Observations carried on in the neighborhood of San Salvador since 1970 on eggs, larvae, pupae and adults of *Hamadryas februa* Hübner are presented, giving an account of the early stage characteristics and developmental times, with photographic illustrations. The foodplants of this and related species are recorded for El Salvador. The behavior of the species is compared with the behavior of other local and South American *Hamadryas* spp. emphasizing the progressive change from solitary to gregarious behavior which the whole group exhibits, with the corresponding adaptations that such a change requires. Impalatability of the species to predators is suggested by the larval foodplant characteristics and the typical non-palatable way the larvae behave.

This is the first article of a third series in which we present our observations on the early stages and adult behavior of butterflies of El Salvador, Central America. Elsewhere a first series has been presented dealing with the local Charaxinae, and in this same journal a second on the Catonephelinae-Callicorinae, all of them subfamilies of the Nymphalidae. Even though there have been earlier descriptions and some illustrations of the early stages of species belonging to this group, e. g. Müller's (1886) and Frühstorfer's (1916), we expect our contribution will be of interest, since new elements are presented.

Our studies on this species started on August 1st, 1970, when one of us (A. M., Jr.) while walking down a road bordering pasturelands, observed a female *Hamadryas februa* Hübner ovipositing on a vine, near the village of Zaragoza (some 15 km SSW of San Salvador). Some eggs were collected and eventually two adults were obtained the 1st and 2nd of September. Since then the species has been reared from the egg a number of times. The eggs and larvae have been put in transparent plastic bags, fresh leaves of the foodplant have been supplied every three days, and the bags cleaned of old leaves and frass every day until pupation. The pupae were transferred to a mosquito-net covered cage until adults emerged. Measurements of each stage and the times elapsed in each phase were recorded, and photos taken of the whole process.

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During the development of the larvae, and during pupation, the bags and cage were kept at all times under ambient light and temperature conditions. Samples of eggs, larvae in the different instars and pupae have been preserved in alcohol to be sent to the American Museum of Natural History, New York, where the adults were determined.

LIFE CYCLE

Egg. Roughly spherical with flattened base and irregular sculpturings; white when recently deposited, darkening before hatching in 5 days. About 1 mm.

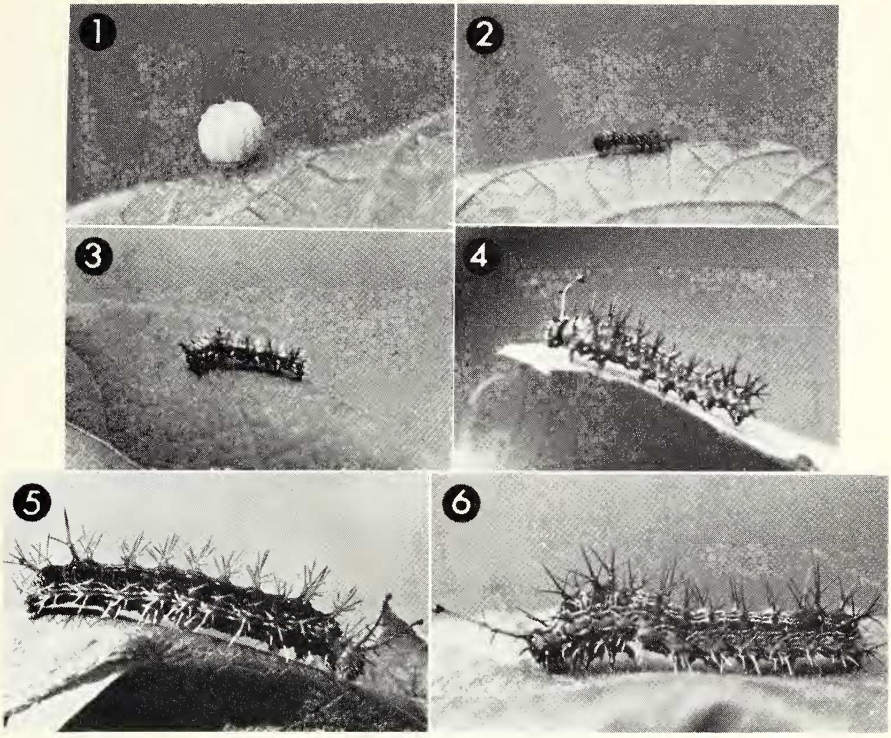
First instar larva. Head faintly cordiform, naked, shiny black. Body cylindrical, brown with scattered white tubercles, legs and prolegs dark brown. About 2.5 mm when recently hatched, 4 mm in 3 days when ready to moult.

Second instar larva. Head shiny black with tiny white spines on anterior and lateral areas of epicrania, sparse short setae on frons and thick, short horns on epicranial apices. The horns are armed basally by 4 tiny spines, and thicken distally. Body brown with transverse rows of furcated spines, very short and alternately dark and light colored. About 7 mm before moulting in 3–5 days.

Third instar larva. Head black with two long black spines laterally and several light and short spines anterad and between the base of the long and slender horns (about three times as long as head), which show basally two short accessory spines directed forward, two longer spines a little higher on the horn shaft and directed outwards, and about the middle of the horn shaft still two other longer spines directed inwards. The horns are each armed distally with a spiny sphere with short setae. Body black with a longitudinal, broken, orange stripe supraventrally, and a profusion of black, forked spines arranged in the following order: on first thoracic segment (T-1) a black cervical shield with two short white spines, one long black forked spine supraspiracularly and a shorter black simple spine subspiracularly; on T-2, a 5-forked black spine subdorsally, a 4-forked supraspiracular spine and a simple spine supraspiracularly; on T-3 a prominent 5-forked subdorsal spine, a 4-forked supraspiracular spine and a simple spine subspiracularly. On first abdominal segment (A-1) a dorsal 3-forked spine, a subdorsal 4-forked spine, a supraspiracular simple spine, a subspiracular 3-forked spine, a supraventral simple spine and finally a simple spine in line with legs and prolegs; A-2 presents one 5-forked dorsal spine, a 5-forked subdorsal spine, a 3-forked supraspiracular spine, a 3-forked subspiracular spine sided by a simple spine, supraventrally one simple spine and two simple spines in line with prolegs. From A-3 to A-6, a 3-forked spine dorsally, a 4-forked subdorsal spine, a 3-forked supraspiracular spine, a 3-forked subspiracular spine sided by a simple spine, and a row of 3 simple spines over the proleg. A-7 as A-6 but with two dorsal forked spines (one behind the other), the first one similar to the preceding ones, the second twice as big and 4-forked. A-8, as A-6 but with only one dorsal, prominent, 5-forked spine deflected posterad. A-9 has only two lateral 5-forked spines directed posterad. Grows to 12 mm in 3–4 days.

Fourth instar larva. Head as in third instar with longer horns. Body as in third instar also, but with several yellow, longitudinal, broken lines dorsally and subdorsally, and orange spots between dorsal and subdorsal spines. Subspiracular and supraventral spines light colored, the rest black. Grows to 18–20 mm in 4–5 days.

Fifth instar larva. Head, when recently moulted, red, turning usually to black after a time. Body mostly black with light green spines, and six yellow, longitudinal, thin stripes from

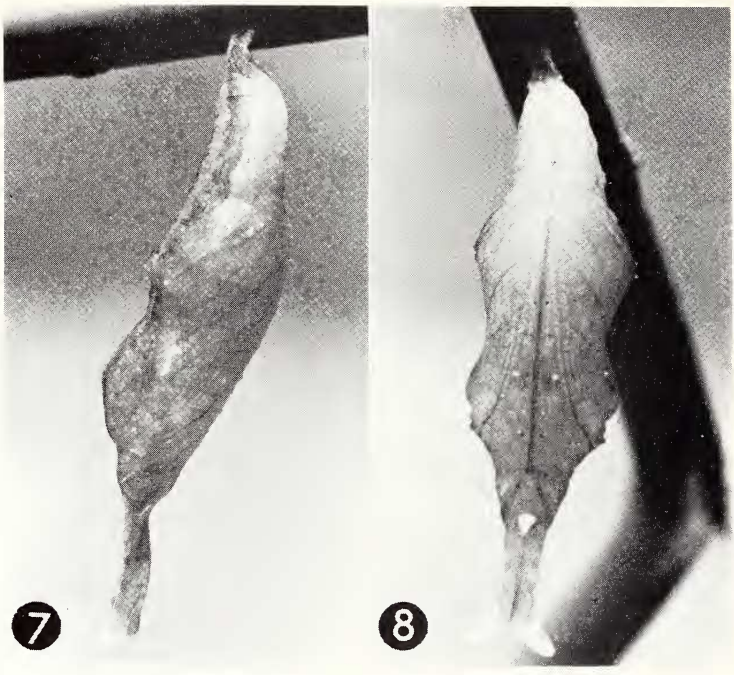


Figs. 1–6. *Hamadryas februa* Hübner. 1. Egg, about 1 mm. 2. First instar larva, 3.5 mm. 3. Second instar larva, 6 mm. 4. Third instar larva, 12 mm. 5. Fourth instar larva, 18 mm. 6. Fifth instar larva, 30 mm.

thorax to abdominal tip, located one at either side of each row of spines; two orange spots at either side of abdominal median spine. At times during this instar, some individuals keep the head red permanently. When this occurs, body shows a reduction of the basic black color, which is substituted by orange. Subdorsal spines prominent, especially T-2, T-3 and A-2, where they have developed a number of small accessory spines on the shaft of the scolus. The same happens on the dorsal spines A-7 and A-8. Grows to 30–32 mm in 4–6 days.

Pre-pupa. Considerably shorter than 5th instar and showing a notable discoloration of the darker shades. In the case of the "orange" morph, becomes almost solid orange. Hangs incurved during 1 day.

Pupa. Variable in color, depending on individuals: some are light brown, some, greenish-brown, some, reddish-brown, with darker touches dorsally and fine, vein-like lines of darker shade ventrally on wingcases. The body thickens gradually from the flat cremaster to the posterior end of the wingcases, which point is the thickest part of the body, then has a dorsal and lateral concavity, then thickens again laterally and forms a slightly keeled hump dorsally. From there the body narrows down to the head, which terminates in two flat, partly fused, then diverging, prolongations, which follow the longitudinal axis of the body,



FIGS. 7–8. *Hamadryas februa* Hübner. 7. Pupa, lateral view, 30 mm. long. 8. Pupa, ventral view.

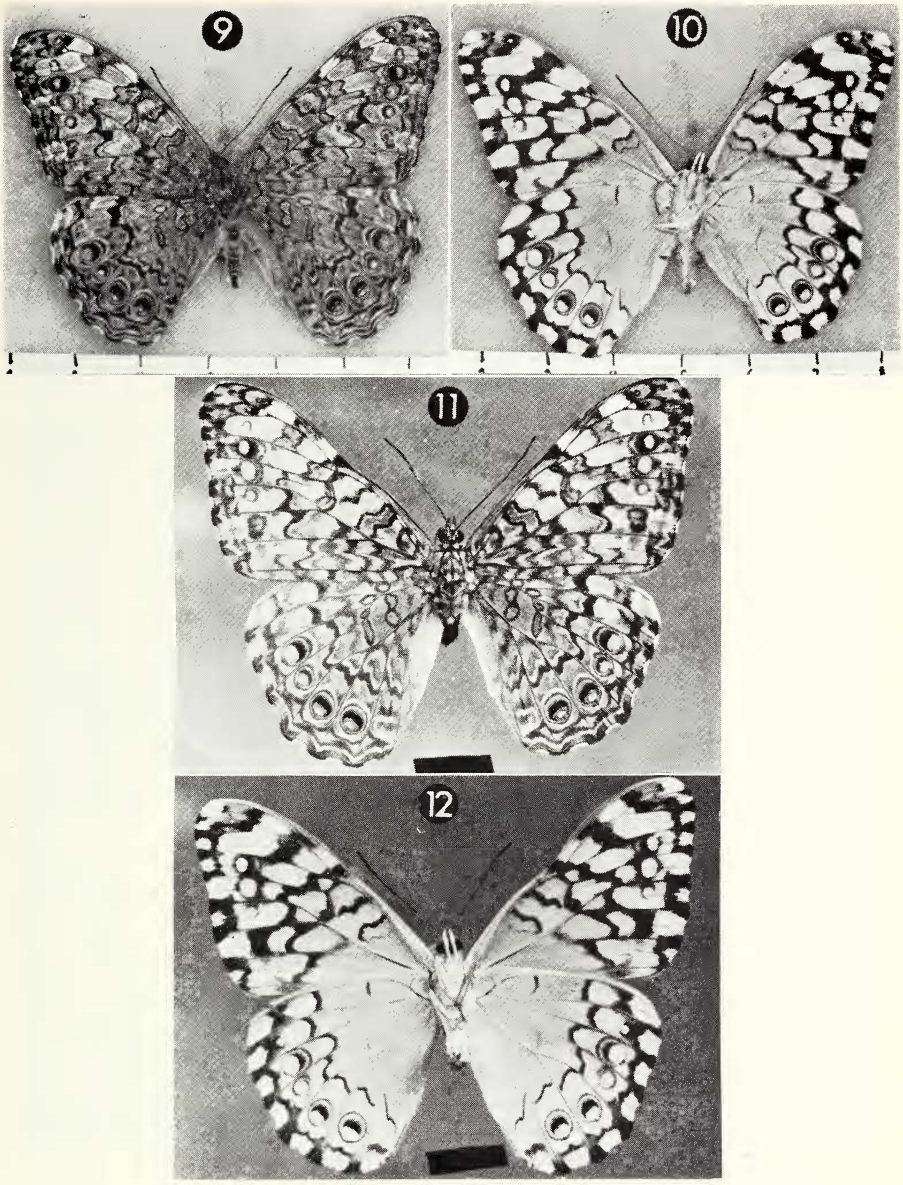
being about ¼ of the total length of the body. Ventrally three small warts are noticeable along either side of the antenna-cases. Measures about 30 mm long by 8.5 mm laterally and 7.5 mm dorso-ventrally at widest points. Durations 6–9 days.

Adults. No sexual dimorphism has been noticed in this species. Forewing shape: costal margin slightly convex, rounded apex, almost straight but sinuose outer margin directed a little inwards, rounded tornus and straight inner margin. Hindwing: almost straight costal margin, rounded outer angle continuing in a convex and faintly sinuose outer margin, rounded anal angle and straight, folded inner margin.

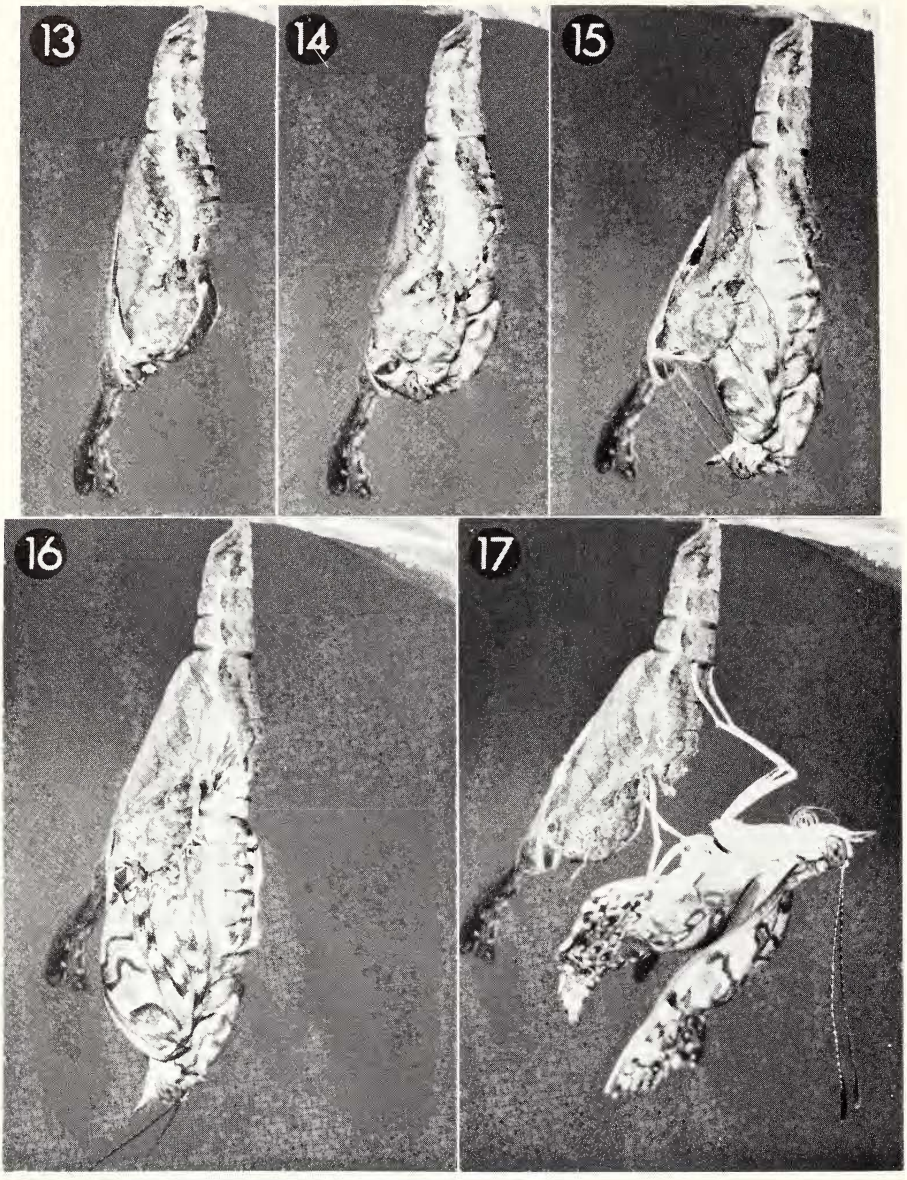
Color dorsally, dominantly light grayish-brown, lighter towards forewing apical zone, with darker brown, sinuose, broken lines and a few circles, forming all a very complicated, practically undescribable pattern. Ventrally mostly whitish-gray with fewer dark brown markings and circles in both wings distally, more so in front wings. Faint orange and yellow bordering basally the crescent shaped spots in the two circles closer to anal angle. Wingspan averages 65 mm in males, 72 mm in females. Complete metamorphosis took from 29 to 38 days.

NATURAL HISTORY

The females of *Hamadryas februa* search for the foodplant along low brushed, open land, flying close to the ground in the neighborhood of wooded areas, until one vine is located. A mature leaf is chosen where the female alights, usually on its underside, and one egg is deposited around the middle of the

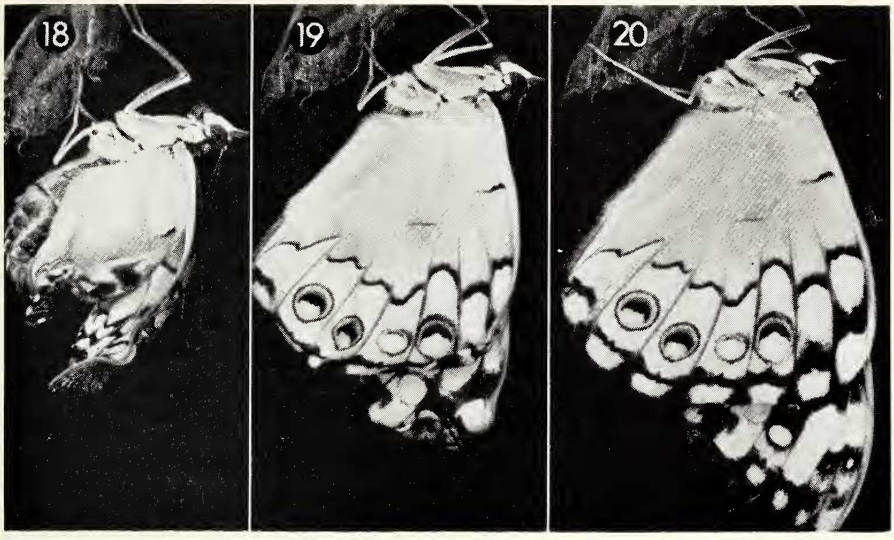


Figs. 9–12. *Hamadryas februa* Hübner. 9 and 10. Male, dorsal and ventral sides. 11 and 12. Female, dorsal and ventral sides. Black bar 10 mm.



FIGS. 13–17. *Hamadryas februa* Hübner. Sequence showing phases of emergence of adult.

leaf. Several eggs are thus deposited on the same plant. It is not unusual that two eggs are laid one on top of the other by the same female (and eventually three), but never have we seen the same female deposit two eggs side by side on the same leaf. In some instances the female alights on top of



Figs. 18–20. *Hamadryas februa* Hübner. Sequence showing gradual expansion of wings following emergence of adult.

a leaf to oviposit. When this occurs, the female moves near the edge of the leaf, and incurving the abdomen, deposits one egg on the underside of the leaf, close to the border.

The tiny larvae, upon hatching, eat from the eggshell just an exit hole, located at the side of it, and leave the rest untouched. They then move to the edge of the leaf and start feeding around a vein (usually at the apex), baring it. The larvae prolong the vein affixing to it their own small frass pellets using their silk as agglutinant. Quite often first, and eventually second instar larvae, are found with several excrement pellets adhering to their own bodies. This behavior might serve a double purpose: camouflage and reserve of materials to lengthen the resting vein when needed. First and second instar larvae are seen through the daylight period resting on their prolonged veins, motionless, head pointing outwards. They only move back to the leaf, late in the afternoon to feed on it. From third instar on, the larvae abandon their perch and move slowly about the plant, on the upper surface of the leaves, weaving a foothold of silk as they crawl, but staying motionless most of the time, with the third thoracic segment humped and the head bent so as to place the horns parallel to the leaf surface. It is not unusual to find more than one larva on the same leaf, but no interaction has been noticed even when they accidentally come in contact. If the larvae are prodded with a blunt object, or teased with a thin flexible one, they end by striking with their horns. When ready to enter pupation, which is announced by a shortening and decoloration of the body,

the larva weaves a mat of silk usually around a thin twig of the foodplant, but at times under a leaf, cleans the digestive tract and hangs from the silken mat by its anal prolegs with head and thorax incurved. After a day the larval skin splits dorsally behind the head and after many body contractions the larval skin is shed and the cremaster anchored firmly by actively wiggling. At first the capital prolongations are limply apposed to the thorax, but after a few minutes they expand forward and position themselves along the longitudinal axis of the body, fusing together their midpart, separated at the base and diverging from each other at the tips. The pupae, usually hanging straight down, wiggle laterally and violently when molested. Their wiggling lasts a few seconds and they then stay bent to one side or the other for a long period of time afterwards. The cremaster of this species (and other related species of the genus), has a flattened base, somewhat as in Catonephelinae, so that it is rigidly applied to the silk button. When the twig is turned upside down, the pupa turns with it staying standing upwards, straight or bent to one side. The day the adult is ready to emerge, the pupa becomes dark gray and the pattern of the wing colors is visible through the pupashell.

The adults rapidly emerge from the pupashell and hang from it ejecting a reddish meconium and unfolding their wings, which are held close together until rigid. It is after their first flight that they learn to keep them spread open most of the time. The adults of *Hamadryas februa* fly actively in, or in the neighborhood of, wooded areas, from about 500 to 1500 m altitude mostly, alighting on tree trunks with their wings spread open and tightly hugging the tree surface, where their gray and brown complicated pattern merges perfectly with the lichen growths which spatter the bark. Males can produce a peculiar loud clicking sound as they fly when meeting other males in flight near their chosen tree, and after an interchange of excited and repeated click-clicks plus many swift circumvolutions, without actually coming in contact, the intruder is chased and the defendant goes back to rest on his lookout, most commonly with the head down. This clicking sound, combined with the aggressive flight, is used also to pursue other approaching butterflies of diverse species, and even dogs, as per repeated observations of one of us (A. M., Jr.). The adults in our cages keep their wings folded at night. In the fields we have seen individuals resting among shrub leaves with their wings folded also, but when alerted by the sound or the shadow of the observer they immediately spread them open. When the adults come to the ground to feed on fermenting fruits, (mangoes, guayavas, rubber-tree fruit, etc.) they sometimes keep their wings open, but at other times the wings are folded. When they feed at wounds on tree-trunks, the wings are always kept spread. We have not noticed the males' clicking sound when they court females, although there is a lot of chasing around.

The preferred local larval foodplant, *Dalechampia scandens* L. and the very

seldom used alternate foodplant, *Tragia volubilis* L. are scandent vines belonging to the Euphorbiaceae, and both have urticant properties when touched with the back of the hand. Either plant is used by other local species of butterflies as larval food. *Dalechampia* besides at least two other species of *Hamadryas*, (probably all of them), is used by *Dynamine* spp., *Catonephele nyctimus* Westwood and *Mestra amymone* Ménétries. *Tragia* is used by *Biblis hyperia* Cramer, *Mestra amymone* and *Dynamine* spp.

The *Dalechampia scandens* vine has coarse, slightly pubescent, alternate, petiolate, tri-lobate and cordate at the base of the leaves; the flower is monoecious, apetalous, with 3 long stemmed pistils surrounded by a host of short stemmed stamens, inside two tri-lobed bracts. The schizocarpous fruits split into three carpels, each bearing one black and brown seed. The fruits are surrounded by long and thin segments covered by a profusion of sharp, fulvous spinulets, which penetrates the skin at the faintest touch.

The *Tragia volubilis* vine shows alternate, petiolate, conspicuously dentate, densely pubescent, shallowly cordate, long leaves. The flowers grow in racemes, and are small, apetalous and produce 3-lobate capsules.

Both plants grow on sunny ground, in low brushed habitats near ravines, road fences and abandoned pieces of land, mostly near wooded areas or coffee plantations. We have found them from about 500 m to about 1500 m altitude. People use them for folklore medicine.

DISCUSSION

The butterflies pertaining to this group have been called at different times by different authors *Peridromia* (Boisduval, 1836), *Ageronia* (Hübner, 1810) and *Hamadryas* (Hübner, 1806), as per information supplied by Dr. A. H. B. Rydon (personal communication). We use the last, which is the older of the three, even if according to Hemming (1967) all three are available generic names.

We are aware of at least two authors describing the early stages of several species belonging to this group (Müller, 1886 and Frühstorfer, 1916), under the name of *Ageronia*. They mention as foodplants for the species they describe, other species of *Dalechampia*. Still, to our knowledge, this is the first description with photographic illustrations of *Hamadryas februa*.

Modern authors usually lump the genus *Hamadryas* within the Nymphalidae, whether in the subfamily Ergolinae (Klots, 1960); in the tribe Ergolini of the subfamily Nymphalinae (Ehrlich & Ehrlich, 1961); or under the subfamily Hamadryadinae (Ebert, 1969). If we were to follow the rule of thumb, which uses egg characteristics to separate the families, we would advocate a family status for this group, as was done, using various nominations, by several authors: Seitz (1915), group K, Ageronidae, which was first used by Doubleday in 1847, and Peridromiidae used by Boisduval in 1836, the latter thus

having priority. The egg shape of the butterflies of the group is quite different from any other egg of the local butterflies. The larvae also are easily recognized, from the third instar on, just by examining the horns of their head. The pupae, even if there are differences in the shape of the head prolongations and the colors between the several species we have seen, are easily identified as *Hamadryas* upon seeing them on account of their peculiar shape.

The females of *H. februa* and its close relative *H. guatemalena* have the same ovipositing behavior: they usually lay one egg at a time, but quite often two, and seldom even three are deposited one on top of the other. According to Müller (1886) (observations on one undetermined species of *Ageronia* and on *A. arete* Doubleday) some species deposit one egg exclusively at a time. His own observations on *A. fornax* were that this species forms a single string of several eggs, one under the other, so that the whole string hangs perpendicularly from the underside of the leaf. Our own observations (and Müller's as well) on *H. amphinome* show that the eggs of this species are also deposited on long strings, forming groups of 3 to 6 strings. It is our feeling that this group of species (*Hamadryas* spp.) is a living example of how natural selection operates: some of the species still have solitary behavior (*arete*); some are in the very process of changing from solitary to gregarious behavior (*februa* and *guatemalena*); one has partially adopted it, forming small groups of 5 to 10 individuals (*fornax*) and another (*amphinome*) has fully adopted gregariousness, with groups up to 45 individuals. Ford (1945) states: "the gregarious habit, determined by the method of egg-laying, is exceptional and carries with it certain noteworthy adaptations." We feel that before the egg-laying method can lead the species to gregarious behavior, there must be a prerequisite *sine qua non* in the larval behavior: the larvae must first abandon the habit of devouring the eggshell upon hatching. If that condition did not pre-exist to the oviposition in clusters, the first individual hatched could destroy at least some, if not many, of the adjacent eggs of the same group, as is the case in solitary species of Lepidoptera, such as *Heliothis zea*, when several females deposit one egg each on the silks of a single corn-ear and the first larva hatched dispose of many eggs close by and even later larvae, (personal observations). We have noticed that this necessary trait of eating just an exit hole from the eggshell is existent in all the local species with gregarious behavior that we have reared: *Battus polydamas* L., *B. laodamas* Felder, *Papilio anchisiades idaeus* Fabr. (Papilionidae); *Chlosyne* spp., *Phyciodes* spp., *Microtia elva* Bates, *Thesalia theona* Ménétries (Melitaeinae); *Actinote* spp. (Acraeinae); *Mechanitis isthmia isthmia* Bates (Ithomiidae); *Caligo memnon* Felder (Brassolidae); *Manataria maculata* Hopff. (Satyridae ?); *Dione juno huascama* Reakirt (Muyshondt, Young & Muyshondt, 1973) (Heliconiidae); *Gynaecia dirce* L. (Coloburinae); *Theritas lisus* (Stoll) (Lycaenidae) and *Hamadryas amphinome* L. In all of these species the hatching larvae eat

just an exit from the micropylar zone of the egg. The exception is *H. amphinome*, which cuts it from the side of the egg, which is of great importance as the eggs are deposited one on top of the other, not side by side as the others do. The same characteristic of not eating the eggshell has also been adopted by several species, which, if not strictly gregarious, have learned to live in a loose community without bellicose interaction, as a result of the need of ovipositing on such restricted areas of the plant as the tender shoots. Even if the females lay only a single egg per location, several females often visit the same plant and thence a number of eggs from several females are accumulated within a very small area. In this group we mention: *Dircenna klugii* Geyer, *Hyposcada virginiana nigricosta* Forbes & Fox, *Tithorea harmonia salvadores* Staudinger, *Hymenitis oto oto* Hewitson (Ithomiidae); *Narope cyllastros testaceae* Godman & Salvin (Brassolidae), all the local species of Heliconiidae (except *Dione juno*, which is gregarious), all the local species of Danaidae (except *Anetia thirsa*, which we have been unable to rear); *Precis genoveva* Stoll, *Anartia fatima* Fab., *A. jatrophae luteipicta* Früh., *Hypanartia lethe* Fab. (which at times deposits one egg on top of another also, as per own observations) (Nymphalidae); *Biblis hyperia* Cramer (Biblinae); *Marpesia* spp. (Marpesiinae); *Pyrrhogyra hypsenor* Godman & Salvin (Muyshondt, 1974 a) (Catonephelinae); *Dynamine* spp. and several species of *Adelpha* (some *Adelpha* very occasionally deposit one egg on top of another also) (Limenitinae), and many species of Pieridae and Lycaenidae. All of these eat the exit hole from the eggshell, and at the most consume a small portion of its wall. Still there are other species which do not devour the eggshell, but have not acquired the tolerance towards other individuals and maintain strict individualistic behavior as larvae, fighting when coming in contact with a neighboring one, with often fatal results to one or the other.

The adaptation of not feeding on the eggshell mentioned, is more remarkable in *Hamadryas februa, H. guatemalena, Hipanartia lethe* and some *Adelpha* sp. where two or more eggs are deposited one on top of the other, as they make the exit hole through the side of the eggshell, which is very important to prevent damage for the egg on top. When two or three eggs are thus laid, the ensuing larvae might at times be found living in the same leaf, even if each one has made its own perch, until the last instar. However they pupate separately.

The habit of baring a vein and prolonging it with excrement pellets (a characteristic shared with several other Nymphalidae) is shown only by the species of *Hamadryas* which deposit the eggs singly (occasionally in twos and threes). This habit has been lost by the gregarious *Hamadryas*, which have developed in place of the cryptical defense against predation that characterizes individualistic species, a rather unpleasant odor, enhanced by the multitude of larvae living in community, plus an irritable temperament which causes the

whole congregation to wiggle convulsively at the faintest provocation. These peculiarities are evidently some of the "noteworthy adaptations" Ford (1945) refers to, that the gregarious species have gone through.

The need to conceal themselves shown by first and second instar larvae of *H. februa* as a defense against predation seems to cease being indispensable to their survival when they reach the third stadium, as evidenced by the desertion of their resting place and crawling openly on the leaves. This unconcerned exposure of themselves seems to indicate that a new means of protection against predation has been acquired in the meantime. Since their foodplants are *Dalechampia scandens* (and *Tragia volubilis*) Euphorbiaceae, which are renown as containing considerable amounts of fluids with poisonous or very caustic properties in many cases, it would not be too daring to deduce that *H. februa* larvae derive from their foodplant predator-deterrent qualities, which take some time to become effective (the time to reach third stadium). Another factor sustaining this notion is the fact that the species is subject to massive parasitism, mostly by Tachinidae. Muyshondt (1973 a, b, 1974, 1975) has pointed out the apparent relationship which exists between parasites and chemically protected larvae, and the behavior of the early stages and adults. Specimens of one tachinid sent to the USDA was determined by Dr. C. W. Sabrosky as "Tachinidae—Gen. sp.—intermediate Eryciinae and Sturniini" with the comment: "Odd species!!". We have obtained up to 4 parasites out of a single larva or pupa.

Even if these factors suggest impalatability, the adult color pattern can be considered a very effective camouflage when they are perched on the sides of tree-trunks with the wings spread open. They seem to have thus a dual defense mechanism: chemical and cryptic.

One of Müller's observations (mentioned also by Seitz) has failed to prove true in our experience. Müller states that the pupae of several *Ageronia-Hamadryas* in his experience are light-sensitive, and would bend their bodies to one side or the other depending on the direction of the sunlight. We have tried several times, at different hours of the day, to induce a reaction from many pupae of various species of *Hamadryas*, including *februa*, exposing them to direct sunlight, then masking the light, for various periods of time, with negative results. What we have noticed is that upon the slightest disturbance the pupae violently wiggle laterally for a short time, and then stop moving with the body bent to one side or the other, which position is kept for long periods of time afterwards.

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